

Avian Predators Target Nocturnal Runs of the Beach-Spawning Marine Fish, California Grunion, *Leuresthes tenuis* (Atherinopsidae)

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Abstract.—Tidal cycles are important cues for many marine and near-shore animals. Birds that typically feed at the water's edge during daytime low tides are rarely present on beaches at night. However, we found that several species of diurnal birds reliably attended and preyed upon the nocturnal spawning runs of a marine fish, *Leuresthes tenuis*, the California Grunion (Teleostei: Atherinopsidae) on the shores of Malibu Lagoon State Beach (MLSB), Los Angeles County, California, USA. Avian hunters of California Grunion included Black-crowned Night Heron *Nycticorax nycticorax*, Great Blue Heron *Ardea herodias*, Snowy Egret *Egretta thula*, and Western Gull *Larus occidentalis*. Spawning runs of California Grunion are synchronized by tides within a narrow window of time, two hours following the semilunar high tides of full and new moons. These silverside fish aggregate *en masse* predictably, and further increase their vulnerability by fully emerging from the water while spawning. This allows the birds to capture California Grunion terrestrially. On nights when spawning runs of California Grunion could potentially occur, birds were present on MLSB, often before the fish began to run onto shore. Number of birds was high for the nights of likely runs whether after full or new moons, whether or not the fish appeared, but not on other nights. We suggest that birds rely on tidal cues to anticipate spawning runs of California Grunion, not the amount of moonlight or the actual presence of fish on shore. Shorebirds were more likely to forage at night at sites close to their upland roosting and nesting areas than at sites with less upland habitat. Observers on nearby Will Rogers State Beach and Topanga State Beach saw comparable spawning runs of California Grunion but reported significantly fewer avian predators. At MLSB, when tide conditions were right, avian predators appeared on the beach with even greater predictability than did their potential prey.

During the remarkable spawning runs of California Grunion *Leuresthes tenuis* (Teleostei: Atherinopsidae), thousands of these silverside fish emerge from the ocean and actively move about on beaches to lay their eggs in the damp sand (Spratt, 1986). These huge aggregations are synchronized by the highest semilunar tides that occur after new and full moons. Although the nights of potential runs are somewhat predictable for human recreational anglers, the runs are highly variable in size and extent, and do not occur on all possible nights or all potential beaches within a single night (Walker, 1952). The actual time of appearance of the fish on shore is usually later than the peak of the tide, and observers report that on many nights with favorable tides, no fish appear at all (Martin et al., 2006). During the spawning season, in the spring and summer months,

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these extreme tides only occur late at night. It has been suggested that the reason for this unusual spawning behavior is that it may provide cover of darkness and less exposure to predators for the adults (Thompson, 1919; Walker, 1952; Spratt, 1986). However, spawning California Grunion attract both marine and terrestrial predators (Gregory, 2001; Sandrozinski, 2013). Large numbers of fishes in a spawning aggregation may attract aquatic predators (Sancho et al., 2000), but during open ocean spawning rushes, with few exceptions, actual take and kills of adult fish are rare (Moyer, 1987).

Shortly after the highest tide, a few nights after the full or new moon, a few California Grunion begin a run by briefly stranding themselves on shore. Dropping out of a receding wave, these marine fish jump and flip about on the sand searching for a mate. If successful, a female digs a hole in the soft, fluid sand with her tail (Martin, 1999; Martin et al., 2004). Upright with only her head still visible at the surface, she emits a clutch of up to 3000 eggs while one or several males surround her, adding milt before both adults return to the ocean on a subsequent wave. Beach spawning with these cryptic nests provides the eggs with good conditions for the developing embryos (Martin et al., 2009, 2011; Martin and Carter, 2013).

California Grunion nest on the sandy beaches of southern California, one of the most heavily populated coastlines of the globe. California beaches host millions of people on summer days, yet at night they are relatively quiet. Some beaches are surrounded by urban development and parking lots, while others are sited in more natural surroundings backed by lagoons and wildlife refuges. Anthropogenic impacts to the spawning grounds abound (Martin et al., 2006, 2013; Matsumoto and Martin, 2008; Martin, 2014). Although the habitat range of this species extends into northern Baja California and the central California coast, over 90% of the species occurs in heavily populated southern California, and the only known spawning habitat for this species is sandy beaches.

Shorebirds and herons are frequently observed on sandy beaches during the daytime, particularly near roosting areas such as lagoons, state parks, and bird sanctuaries. Most birds are visual predators, so foraging depends on available light and is usually diurnal, with some exceptions. Many herons eat fishes and are important intertidal predators, particularly during daytime low tides (Feunteun and Marion, 1994; Hoyer and Canfield, 1994). However, some shorebirds that forage at low tides may be active at night, even during very dark nights (Robert et al., 1989; McNeil et al., 1993; Dwyer et al., 2013).

With tide charts, humans can expect spawning runs of California Grunion within two hours after the highest tides following each full or new moon during the spawning season, March through August (Walker, 1949). Grunion spawn on the four nights after both new moon and full moons, and overcast skies that obscure the moon do not deter the runs (Walker, 1952). However, any or all nights may pass without a spawning run at any given beach. The strength of runs of California Grunion is variable from night to night, between beaches on a given night, and within and across seasons (Walker, 1949; personal observations). During smaller runs, California Grunion may be seen in the waves and some occasionally strand for brief periods without spawning. Actual runs, with numerous fish emerged out of water onto shore, occur on fewer than 50% of the nights when tides are favorable (unpublished data from Grunion Greeters). Outside of this period, no runs occur because the oviposition site is not accessible (Martin and Swiderski, 2001; Martin et al., 2004).

During nights of potential spawning runs of California Grunion, several species of herons and other birds have been observed at the high tides, apparently watching the waves in the dark and sometimes wading into the surf. The regular appearance of avian

predators, even before California Grunion start appearing on shore, suggests that birds may be able to anticipate runs in advance of seeing fish emerge. Once the run starts, these birds begin to catch fish. Nocturnal foraging may be affected by the light from the moon. For example, nocturnal foraging by shorebirds increases on nights with a visible moon (Dodd and Colwell, 1998). Nocturnal behavior and foraging change with the moon phase for many nocturnal birds, including Common Cranes *Grus grus* (Alonso et al., 1985), Common Poorwills *Phalaenoptilus nuttallii* (Mills, 1986; Brigham and Barclay, 1992; Woods and Brigham, 2008), and Australian Owlet-nightjars *Aegotheles cristatus* (Brigham et al., 1999).

Tidal cycles affect avian predators' access to marine prey resources. Many wading birds and shorebirds feed at low tides. Relatively few feed at high tides because marine organisms generally are covered by water. Because the lunar day is about 24 h 45 min long, the lowest and highest tides occur later on subsequent days. Diurnal animals that forage tidally may need to be able to feed at night occasionally. For example, at low tides, most species of shorebirds in a tidal lagoon foraged with comparable frequency during the day or at night (Robert et al., 1989), and Grey Herons *Ardea cinerea* arrived to feed at low tides early in the morning before sunrise (Sawara et al., 1990). Great Blue Herons *A. herodias* and Black-crowned Night Herons *Nycticorax nycticorax* fed during low tides after sunset in a salt marsh (Black and Collopy, 1982). During migrations, Semipalmated Sandpipers *Calidris pusilla* foraged on intertidal amphipods during nighttime low tides (McCurdy et al., 1997).

We tested the following hypotheses. First, we hypothesized that the birds would be present on the beach at night only when tides were favorable for spawning runs of California Grunion, but not on other nights. Following up, a second hypothesis was that these birds use tidal cues to determine appropriate nights, rather than either waiting for the arrival of fish on shore, or observing the available moonlight. Because the number of birds present at Malibu Lagoon State Beach can be large, we hypothesized that the number of avian predators during spawning runs of California Grunion may be correlated with adjacent upland habitat for wildlife. Thus Hypothesis 3 was that the number of birds present for spawning runs of California Grunion would be smaller at nearby beaches with similar California Grunion runs but less upland bird habitat.

Materials and Methods

Field observations were made at three locations within a 20 km linear segment of the shore in Los Angeles County, California. All three wide, sandy recreational beaches abut Pacific Coast Highway, a major thoroughfare lined with streetlights, and all support significant spawning runs of California Grunion. The first site is Malibu Lagoon "Surfrider" State Beach (34°02'07" N, 118°40'42" W). Adjacent to a restored coastal lagoon of Malibu Creek, MLSB is a roosting, feeding, and nesting area for up to 256 species of birds (Cooper, personal communication). The second, Topanga State Beach (34°02'15" N, 118°34'58" W), is a bluff-backed beach around a small, 1 acre seasonal lagoon at the outlet of Topanga Creek. TSB includes a narrow upland area with some trees and riparian habitat that extends shoreward for several miles through a canyon. The third, Will Rogers State Beach at Sunset Boulevard (34°02'16" N, 118°33'24" W) is an urban beach with no creek or upland natural habitat. Sandy WRSB is backed by rip rap, parking lots, a restaurant, a mini-mall, houses, and extensive urban development in the adjacent area shoreward of Pacific Coast Highway. The lights from the highway do not

illuminate the shoreline where runs occur, but each beach has small areas of the shoreline lit artificially by structures such as restaurants or a pier.

For Hypotheses 1 and 2, birds and California Grunion were observed by the authors for 27 nights from May to July, 1996 at MLSB. Observations were made for two hours between 2100 and 0100 starting at the time of the highest nocturnal tide, for seven sequential nights every two weeks. Observations started before any fish appeared on shore, and continued for up to two hours, ending either after the California Grunion departed, or all the birds left. Avian species on the beach were identified, counted, and observed for predatory behavior with a night vision monocular (ITT night mariner 160 Generation III), supplemented by occasional use of binoculars and a flashlight. Walking shoreward of the high tide, the observers were able to walk along the length of the shoreline with minimal disturbance to the birds at the water line.

For Hypotheses 2 and 3, the authors and volunteer Grunion Greeters observed three local beaches between the years 2004 and 2010. Award-winning citizen scientists, the Grunion Greeters have been observing runs of California Grunion since 2002 (Martin et al., 2006, 2007). These volunteers received training to observe and input data through a web-based portal at www.Grunion.org for specific nights and locations during spring and summer. Observations were made for two hours, starting at the high tide, between 2100 and 0100, following each full and new moon in April, May, and early June. Data gathered from 2004 to 2010 included a rating of the approximate number of fish on shore at the peak of the run using the Walker Scale, the duration of the run, the extent of shore involved, and the activity of the fish. Along with data on the California Grunion, observers noted weather conditions, cloud cover, wave action, presence of people including anglers, and the presence of birds and other predators. Observations were made in April, May, and June on the 10 nights per year when runs of California Grunion were most likely to occur, for a total of 86 run series observations. Malibu Lagoon State Beach was observed on ten additional summer nights when spawning runs were neither predicted nor seen in 2010. The strength and duration of spawning runs of California Grunion on shore were evaluated according to the Walker Scale (Martin, 2014; www.Grunion.org). Scores ranged from W-0, no fish or only a few fish on shore, to W-5, thousands of fish covering an extensive area of shoreline at peak levels for over an hour. Data were compared using the highest value of one semilunar tide series on each beach.

Results

On nights with tides conducive to a spawning run of California Grunion, large numbers of birds were present on shore at Malibu Lagoon State Beach (MLSB), but they were absent on other nights (Fig. 1), supporting Hypothesis 1. No California Grunion appeared on the shore on any night that was outside the forecast window ($N = 21$). A few California Grunion sometimes appeared on the night of a new or full moon, and larger runs occurred on subsequent nights. No California Grunion appeared before the night of a full or new moon; zero or just a few birds were present on this first night of each observation series at MLSB, as on other nights when no runs were expected.

On subsequent nights after the new and full moons, dozens of birds in a mixed flock appeared on the shores of MLSB. This happened for several nights during the tides that were favorable for California Grunion runs. After the fourth night following a full or new moon (the fifth night of each observation series), numbers of birds significantly declined, and birds remained scarce at night until the next semilunar high tide. The most common birds seen at the tides appropriate for spawning runs were three herons (Ardeidae) and

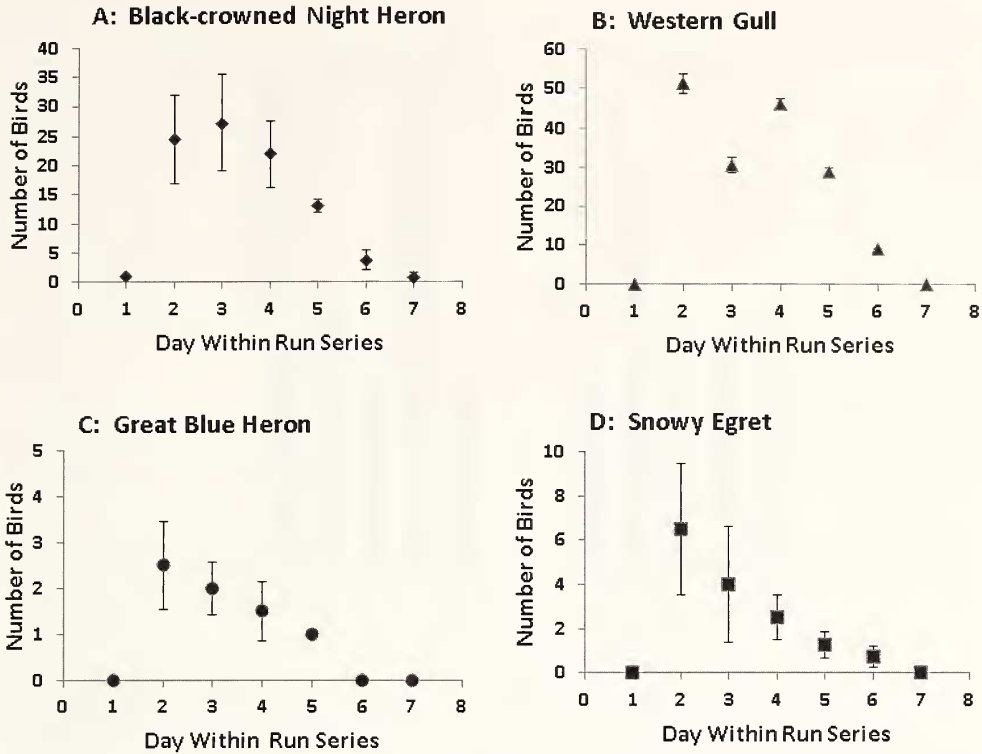


Fig. 1. The most common birds seen during spawning runs of California Grunion at Malibu Lagoon State Beach were (A) Black-crowned Night Heron *Nycticorax nycticorax*, (B) Western Gulls *Larus occidentalis*, (C) Great Blue Herons *Ardea herodias*, and (D) Snowy Egrets *Egretta thula*. Observation Night 2 is the night of the full or new moon phase, typically the highest semilunar tide. Numbers of birds (mean \pm S.D.) on nights 2–5 were significantly greater than at other times or on other nights before or after the predicted runs. Note the different scales on the y-axis for each graph.

gulls (Laridae). The species seen most reliably and in greatest numbers were Black-crowned Night Heron (Fig. 1A), and Western Gull *Larus occidentalis* (Fig. 1B). Great Blue Heron (Fig. 1C) and Snowy Egret *Egretta thula* (Fig. 1D), were also commonly seen during the initial year of this study. Heermann's Gulls *L. heermanni* and California Gulls *L. californicus* were occasionally seen. All gull species were counted together because the individual species were difficult to distinguish reliably in low light at night.

At MLSB, the strength of the spawning run of California Grunion on shore, as indicated by the Walker score, had little effect on the presence or absence of the birds (Figure 2), supporting Hypothesis 2. If the tides were right, even on nights when no fish emerged from the waves to spawn on the beach, birds were still present on shore at night, often for several hours. In addition, the amount of moonlight did not affect the number of birds observed on these nights. Over the course of the study, on the nights of a potential run series, the number of birds was not different whether there was a new or a full moon (t-test, $df = 16$, $t = -0.355$, $p = 0.73$).

The runs of California Grunion were comparably large on the three study beaches. Runs of different strengths sometimes occurred on multiple nights of a series on each beach. Walker Scores for runs on both MLSB ($N = 35$) and WRSB ($N = 27$) did not differ (Wilcoxon Signed Rank test, $W = 5$, $z = 0.12$, $p = 0.90$). Both beaches had the

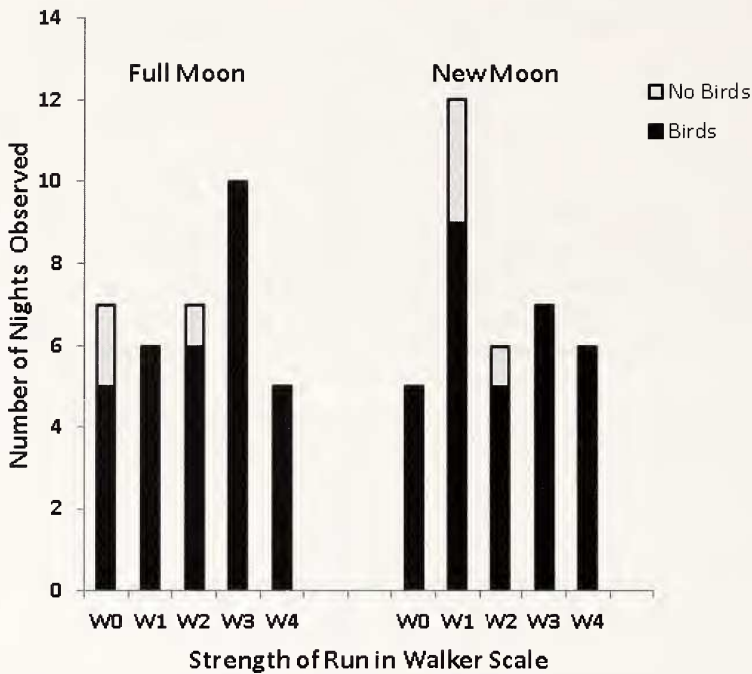


Fig. 2. The magnitude of spawning runs of California Grunion *Leuresthes tenuis*, as measured by the Walker Scale, does not affect the presence or absence of predatory birds at Malibu Lagoon State Beach. Nor does the amount of moonlight. Birds were present at MLSB on at least 90% of the nights when tides were conducive to spawning runs, whether after a full or a new moon.

same median and mode run size, with a Walker score of W-3. The median and mode Walker Score at TSB was W-4 ($N = 26$), significantly higher than at MLSB over the course of the observations (Wilcoxon Signed Rank test, $W = -165$, $z = -2.5$, $p = 0.01$). More than half the time, the size of the spawning runs of California Grunion at MLSB were smaller than the runs at one or both of the other two nearby beaches.

Although the runs of California Grunion are highly variable, semilunar tides appropriate for runs were positively and significantly correlated with the actual appearance of fish on shore on all three beaches (Fig. 3). On the other hand, the hunting birds appeared much more reliably on nights with appropriate tides at MLSB than at either TSB or WRSB (Table 1). At MLSB, the correlation between presence of birds and appropriate tides with potential runs was higher ($Rho = 0.91$, $p < 0.03$) than the correlation between bird presence and California Grunion presence on shore ($Rho = 0.48$, $p = 0.24$). However, on TSB birds were more likely to appear on nights when the fish actually appeared on shore ($Rho = 0.85$, $p < 0.04$) than on any night with appropriate tides but no run ($Rho = 0.70$, $p = 0.09$).

The number of birds present was significantly different at the three study sites during nights of potential spawning runs (Fig. 4), supporting Hypothesis 3. At MLSB, on average 74.5 ± 16.1 birds attended nights of potential runs, and birds were present on at least 90% of the nights that had tides appropriate for spawning runs. On other nights with less favorable tides, very few birds were seen on the shores of MLSB (t-test, $t = 5.12$, $df = 34$, $p < 0.0001$). At TSB, fewer birds were present than at MLSB during California Grunion runs (Mann Whitney U test, $U = 1.5$, $z = 3.91$, $p < 0.0001$). At TSB only 6.55

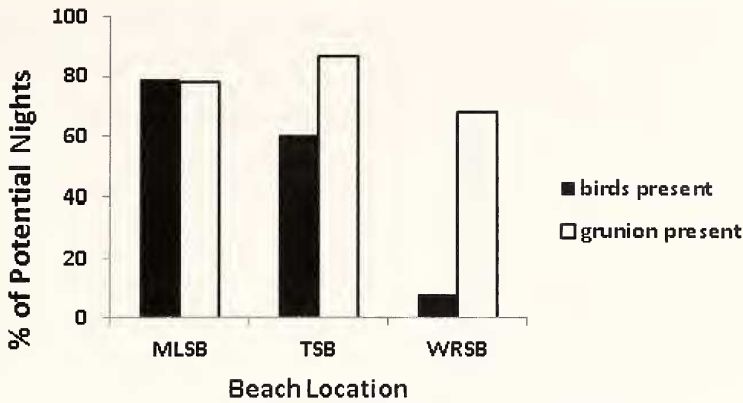


Fig. 3. On nights when tides were conducive to spawning runs, the majority of observers on all three beaches reported the presence of California Grunion. Birds were far more likely to be present on Malibu Lagoon State Beach (MLSB) than on Topanga State Beach (TSB) or Will Rogers State Beach (WRSB).

+/- 1.9 birds, usually Black-crowned Night Herons, attended runs (Fig. 4). At WRSB, birds were almost never seen during California Grunion runs, and those that did appear were always alone. On TSB, birds were occasionally seen, only on nights when the California Grunion emerged onto shore ($Rho = 0.85, p < 0.04$), and not when there were appropriate tides but no fish present ($Rho = 0.70, p = 0.09$). In a W0 run, when no fish actually spawned on the beach, some fish congregated in the water near shore and were sometimes caught by birds, although on many nights with appropriate tides, no California Grunion appeared at all. Members of all bird species present during the runs were observed eating California Grunion directly off the sand. When one California Grunion emerged from a wave onto the sand during a run, any bird that was nearby ran to it and attempted to grab it. In some cases the fish was caught just as it emerged; in other cases the fish was actively spawning; rarely a fish was stranded by a large wave pushing it high on shore. California Grunion are able to jump and move about on land to some extent, and this allowed a few to escape predation. No predation occurred in water deeper than a few centimeters in the wave wash, as the fish were able to swim quickly to safety. No bird was observed preying on anything but California Grunion during these runs.

Black-crowned Night Heron was the first species to arrive on any night, and the most persistent in remaining. This species usually arrived about half an hour before the highest

Table 1. Spearman Rank Correlations at three state beaches in Los Angeles County for nights when tides are appropriate for California Grunion runs, as compared with actual spawning runs of California Grunion, and as compared with presence or absence of predatory birds on shore. Asterisks and bold type indicate significant correlations ($P < 0.05$).

Correlations	Malibu Lagoon SB	Topanga SB	Will Rogers SB
Appropriate tides vs. presence of California Grunion	$Rho = 0.64, P = 0.12$	$Rho = 0.70, P = 0.09$	$Rho = 0.76, P = 0.06$
Appropriate tides vs. presence of birds on shore	$Rho = 0.91, P = 0.03^*$	$Rho = 0.70, P = 0.09$	$Rho = 0.19, P = 0.64$
Presence of birds on shore vs. presence of California Grunion	$Rho = 0.48, P = 0.24$	$Rho = 0.85, P = .04^*$	$Rho = 0.05, P = 0.91$

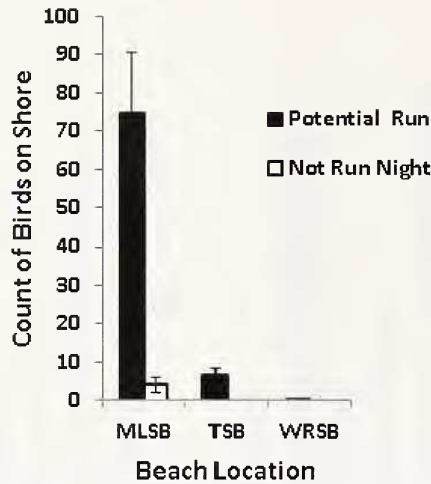


Fig. 4. Significantly more birds were present at Malibu Lagoon State Beach (MLSB) during nights of potential California Grunion runs, than on nights when runs are unlikely to occur. For California Grunion runs of similar sizes at nearby Topanga State Beach (TSB) and Will Rogers State Beach (WRSB), significantly fewer birds were observed. Different letters indicate significant differences.

tide and formed a single line of individuals spaced a meter or more apart, facing the waves along shore. Each stood quietly on the dry sand watching the waves until fish began to appear momentarily in receding waves. When a fish was sighted in a wave returning to the ocean, the Black-crowned Night Herons ran down the sand toward the water and usually caught the fish before it washed away into deeper water. Some faced away from the ocean with the back to the wave, letting the water wash up from behind under them. If a fish dropped out onto the sand as the wave receded, it was caught. If disturbed or if unsuccessful in one location, Black-crowned Night Herons flew through the darkness over water to another location on the beach. They sometimes called while flying over the surf at night, especially when conspecifics were actively feeding during a run. Closer to the water, Great Blue Herons and Snowy Egrets stood in the swash zone of incoming waves. Great Blue Herons, with longer legs, waded in deeper. Both species watched the water, and when a fish was spotted, caught it by spearing with the bill. After a successful catch, herons often moved a few steps up the shore out of reach of the waves, to manipulate the fish in the beak for swallowing. In the initial year of observations, gulls and Snowy Egrets were regularly present on shore at MLSB at night during spawning runs of California Grunion. Since 2004, fewer gulls and no Snowy Egrets appeared at night on MLSB, yet Black-crowned Night Herons and Great Blue Herons have been present consistently during spawning runs across the years. In the daytime, large numbers of gulls and Snowy Egrets are easily observed on MLSB and adjacent Malibu Lagoon.

Discussion

Avian predators are present on Malibu Lagoon State Beach (MLSB) during the nights of potential spawning runs of California Grunion, but not on other nights (Fig. 1), supporting our first hypothesis. Spawning runs of California Grunion provide a very temporary but bounteous and moderately predictable resource on sandy shores during nocturnal high tides. For birds that may rarely hunt at night, even a small run can provide ample food for a successful predator. Black-crowned Night Herons and Great

Blue Herons were reliably seen on nights following semilunar high tides (Fig. 1A and C). They arrived on the beach earlier than fish did, and birds were on the beach at MLSB on nearly all nights when the tides were appropriate, more frequently than the California Grunion were. However, these birds were not on the beach on other nights, when no run would be expected.

No matter how many or few fish actually appeared on shore, regardless of available moonlight, birds were present, waiting on shore before the fish emerged from the waves at MLSB. The bird species that appeared most consistently was Black-crowned Night Heron (Fig. 1). Black-crowned Night Herons have large eyes, special pigments, and a wide field of vision that enable them to forage for fish and amphibians during day and night (Katzir and Martin, 1998). They prey on tern and other bird colonies at night (Hunter and Morris, 1976; Brunton, 1997, 1999). Great Blue Herons are also known to forage at night (Black and Collopy, 1982). Black-crowned Night Herons and Great Blue Herons remained fairly consistent visitors at MLSB over the years of this study. These two species also attend California Grunion runs at other California beaches (Grunion Greeters, personal communication).

Snowy Egrets were frequently present in the first year of the study at MLSB, although in smaller numbers than the other species (Fig. 1D). Snowy Egrets no longer attend California Grunion runs at MLSB, with no reports since 2004, although a few individuals have been seen at other California beaches during runs (Grunion Greeters, personal communication). Many individuals in this species forage nearby in shallow wetlands such as Malibu Lagoon during the daytime, and also at the beach during low tides in daylight (Cooper, personal communication). Snowy Egrets generally feed in shallow water by stirring up fish with their feet; this species does not forage at high tide as a rule (Master et al., 2005). However, a California Grunion run is not a typical prey resource, so some individual Snowy Egrets have sometimes been able to take advantage of this opportunity.

Another avian predator on California Grunion runs was documented sixty years ago. Up to 30 Barn Owls *Tyto alba* at one time were seen feeding on beach spawning runs of California Grunion in northern San Diego County, California (Gallup, 1949). This nocturnal predator is a common bird in open areas, and still occurs in coastal areas of California near beaches where California Grunion run, for example at Camp Pendleton in northern San Diego County, and in Malibu. However there have been no reports of Barn Owls at any runs of California Grunion in any location throughout the species range, over thousands of observations in the past ten years (Grunion Greeters, personal communication).

Birds appear to be able to recognize tidal cues on the nights when this resource may arrive, rather than light cues from the moon (Fig. 2) or the actual presence of fish on shore (Fig. 3). For visual predators including most birds, amount of available light is critical (Jetz et al., 2003). Light cues differ between the full and new moon phases. However, available moonlight had little effect on the presence or absence of birds during tides for spawning runs at MLSB. Birds were equally likely to be present after either new or full moon runs and on overcast nights, early or late in the four-night run series, at any strength of run (Fig. 2). This suggests these birds are more influenced by tidal height than by amount of moonlight or presence of fish out of water, supporting our second hypothesis. On the other hand, the nocturnal activity of Elf Owls *Micrathene whitneyi* and Western Screech Owls *Megascops kennicottii* does not depend on moon phase (Hardy and Morrison, 2000). White-chinned Petrels *Procellaria aequinoctialis* forage widely in the Southern Ocean during day and night while incubating eggs, with no influence of

moon phase (Weimerskirch et al., 1998). Shorebirds usually forage in daytime, but short days in winter may not be sufficient for gathering food so some nighttime foraging occurs, even when there is no moonlight (Pienkowski et al., 1984).

Longline fishermen report that birds are much more likely to be caught on nights with bright moonlight than when there is no moonlight (Brothers *et al.*, 2000; Moreno and Rubilar, 1996). Shy Albatross *Thalassarche cauta* also feed more during full moons, flying faster and farther on those nights than on dark nights (Hedd et al., 2001). At colonies of Black-vented Shearwater (*Puffinus opisthomelas*), gull predation occurs during moonlit but not dark nights (Keitt et al., 2004). Gull predation is also heavier during the full moon phase for Cassin's Auklets *Ptychoramphus aleuticus* (Nelson, 1989).

Artificial lights may impact foraging ability of wildlife at night (Rich and Longcore, 2006), either by increased effectiveness (Dwyer et al., 2013), or by increased risk of predation to animals that are active at night. Terrestrial insectivorous birds are attracted to powerful artificial lights for foraging (Lebbin et al., 2007). Wading birds increase foraging time and effectiveness with artificial lighting (Santos et al., 2010), and Black-crowned Night Herons are known to use intense shoreline illumination to forage at night in a salt marsh (Erwin et al., 1990). In the present study at MLSB, artificial lighting from street lights and a pier provide some illumination onto some areas of the beach where the avian predators were observed, and may contribute to the lack of effect of moon phase on their behavior. However this light is quite dim at the water's edge where the runs occurred. Occasionally observers used flashlights to see California Grunion on shore, and the birds quickly began to use the beams of light to assist their own prey capture.

Shorebirds rarely forage along the shoreline at high tide (Burger and Olla, 1984). However, spawning aggregations of the beach spawning Atlantic Silverside fish *Menidia menidia* occur during diurnal high tides, attracting avian species that prey on them in shallow water over seagrass beds (Middaugh, 1981). A congener of California Grunion, the Gulf Grunion *L. sardina*, spawns on sandy beaches in the Gulf of California, where some of the high tides appropriate for spawning occur in the daytime (Thomson and Muench, 1976). Avian predation is very intense on these daytime runs. Because of low wave energy at the top of this enclosed bay, Gulf Grunion spawn at the water's edge rather than out of water like California Grunion. Birds such as Brown Pelican *Pelicanus occidentalis*, cormorant *Phalacrocorax sp.*, and several species of gulls, *L. occidentalis*, *L. delawarensis*, *L. californicus*, *L. heermanni*, and *L. atricilla*, dive to feed on the fish in shallow water (Thomson and Muench, 1976), rather than catching them emerged on shore. The species of avian predators and their behavior during this aerial attack on Gulf Grunion differ from the species and their terrestrial hunting seen during nocturnal predation on California Grunion out of water.

Conclusions

Number of birds present during California Grunion runs was site-specific, much higher on MLSB than at two nearby beaches with equal or stronger runs. The comparison beaches, WRSB and TSB, are both adjacent to Pacific Coast Highway and both have restaurants and other structures with some outdoor lighting. However, these locations held far fewer avian predators. During nights when California Grunion runs were forecast, large numbers of birds were consistently present at MLSB, but only a few were seen occasionally at Topanga State Beach (TSB), and almost no birds attended California Grunion runs at Will Rogers State Beach (WRSB) (Fig. 3). At TSB, the avian species most consistently seen during the runs of California Grunion was Black-crowned Night

Heron, followed by Great Blue Heron, although in much smaller numbers than at MLSB (Fig. 4). As described earlier, the upland habitat around MLSB is far more extensive than at TSB or WRSB, creating a shorter distance for birds to fly from roosts to the beach at night.

In summary, birds, particularly Black-crowned Night Herons and Great Blue Herons, fed on nocturnal spawning runs of California Grunion and were reliably seen at tide-synchronized times of potential spawning runs, whether or not the fish actually appeared. When tide conditions were right, these avian predators appeared on the beach with even greater predictability than did their potential prey, the spawning fish.

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